Does the climate of the origin control anatomical characteristics of the vessel elements as well as different foliar traits in *Fagus crenata*?

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ABSTRACT: The relationships between climatic factors and anatomical characteristics of the vessel elements as well as different foliar traits were investigated in *Fagus crenata* seedlings originating from different provenances. *Fagus crenata* samples were prepared from Chichibu Research Forest of Tokyo University. In the present study, vessel number per mm^2, average vessel diameter, vessel area percentage, vessel element length, percentages of perforation plate types, transpiration rate, stomatal conductance, leaf area, leaf thickness, leaf dry mass per unit leaf area, stomatal density and stomatal pore length were measured. Vessel number per mm^2, vessel area percentage, stomatal conductance, transpiration rate, leaf thickness and leaf dry mass per unit leaf area showed a significant negative correlation with yearly, winter, spring and autumn precipitation. The majority of the studied characteristics were not related to the mean annual and seasonal temperatures of the original provenances. The results suggest that anatomical characteristics of vessel elements and different foliar traits in *Fagus crenata* are mainly influenced by the precipitation of the origins.

Keywords: climate; *Fagus crenata*; foliar traits; vessel elements

Fagus crenata Blume, also called Buna or Siebold's beech, is an endemic diffuse porous hardwood that commonly dominates Japanese cool temperate forests (Horikawa 1972; Ohwi, Kitagawa 1992). It is widely distributed from the Kuromatsunai lowland in Hokkaido to Takakuma in Kyushu. Environmental conditions are different within the area of its distribution, for example beech forests on the Pacific side are exposed to wind storms more frequently than those on the Japan Sea side (Uchida et al. 1983; Cao, Ohkubo 1999); however, on the Japan Sea side they experience heavy annual snowfall (2–3 m) (Homma 1997; Cao, Ohkubo 1999). Finding out the dissimilarities in different characteristics of *Fagus crenata* has therefore been a great interest of many researchers (e.g. Hiura 1993; Homma 1997; Koike, Maruyama 1998; Koyama et al. 2002; Bayramzadeh et al. 2008).

Previous studies showed that anatomical characteristics of the vessel elements and morphological, anatomical as well as physiological characteristics of leaves are different not only within the area of *Fagus crenata* distribution but also in the seedlings originating from different provenances and grown under uniform environmental conditions (Hiura 1993; Koike, Maruyama 1998; Koyama et al. 2002; Bayramzadeh et al. 2008).

It is supposed that there are relationships between the variations of the climatic factors of the seed origins and the mentioned variations in *Fagus crenata* since it is a climatic climax species (Horikawa 1972; Matsui et al. 2004). However, the main climatic factors which are related to the variations of the vessel element anatomy and different foliar traits have remained unclear up to now.

Therefore, this study was designed to determine the main climatic factors of the original seed sources in the past related to the variations of the vessel element anatomy and different foliar traits in the *Fagus crenata* seedlings originating from different provenances and grown under uniform environmental conditions.

As previous research showed that the variations of the anatomical characteristics of the vessel elements within the sapwood area were in correspondence with the variations of foliar traits in *Fagus crenata* (Bayramzadeh et al. 2008), the relationships between variations of the vessel element anatomy and climatic factors were investigated in all annual rings occurring within sapwood area. Such a kind of studies is useful to explore the ecological patterns on an almost whole tree level.

MATERIAL AND METHODS

Study site and plant materials

We used 13-year-old *Fagus crenata* seedlings grown from the seeds that had been collected from seven different provenances in Honshu Island, Japan namely, Kurikomayama, Nishikawa, Oohirahara, Hiruzen, Ogawa, Minakami, and Chichibu. The seeds of the above-mentioned regions after collection were sown into plastic pots (20 cm in diameter), filled with local soil and grown for two years on the beech forest floor in Chichibu. In 1992, the saplings were transplanted to 1.5 × 1.5 m quadrants in an experimental nursery in Chichibu Research Forest of the Tokyo University (35°59'N, 139°04'E) and disturbed soil was covered with litter. Detailed information about the characteristics of the studied provenances is given in Fig. 1 and Table 1. Climatic factors of the studied provenances were deduced from the records of the nearest meteorological stations.

Anatomical measurements of the vessel elements

Four seedlings of each provenance picked up at random were selected for anatomical measurements of the vessel elements. A five-centimetre disc was cut from the main stem 90 cm above the base. Our primitive experiments showed that ray and axial parenchyma cells in the first ring adjacent to the pith contained starch granules (Figure not shown) and we concluded that all rings from the pith side to the bark side belonged to sapwood. Thus, anatomical characteristics of the vessel elements were measured in all annual rings.

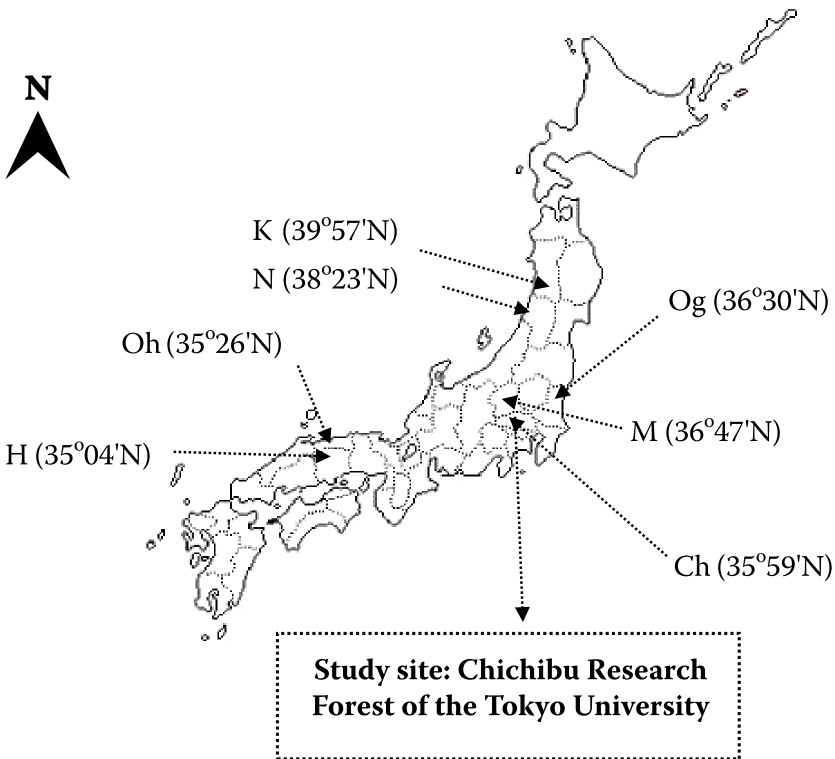

Fig. 1. Locations of the study site and provenances of *Fagus crenata* studied in this research: Kurikomayama (K), Nishikawa (N), Oohirahara (Oh), Hiruzen (H), Ogawa (Og), Minakami (M), and Chichibu (Ch)

Table 1. Climatic factors of *Fagus crenata* provenances extracted from the climate database generated by Japan Meteorological Agency (the data are means from 1971 to 2000)

Provenance	YP (mm)	MAT (°C)	SP[1] (mm)	ST[1] (°C)	SUP[2] (mm)	SUT[2] (°C)	AUP[3] (mm)	AUT[3] (°C)	WP[4] (mm)	WT[4] (°C)
Kurikomayama	2,079	8.3	436	5.9	787	18.3	551	10.8	304	–1.9
Nishikawa	2,715	8.6	449	5.6	605	19.4	825	10.8	835	–1.5
Oohirahara	1,789	14.7	349	12.4	558	24.3	484	16.7	397	5.1
Hiruzen	1,291	13.7	359	11.8	495	24.1	317	15.5	118	3.2
Ogawa	1,229	9.7	325	7.5	420	18.5	383	12.1	99	0.3
Minakami	1,692	10.2	353	7.9	512	20.6	420	12.4	406	–0.2
Chichibu	1,262	12.8	242	11.3	517	22.9	412	14.6	89	2.2

YP – yearly precipitation; MAT – mean annual temperature; SP – spring precipitation; ST – mean spring temperature; SUP – summer precipitation; SUT – mean summer temperature; AUP – autumn precipitation; AUT – mean autumn temperature; WP – winter precipitation; WT – mean winter temperature

[1]March, April, May; [2]Jun, July, August; [3]September, October, November; [4]December, January, February

For measurements of vessel diameter, vessel number per mm^2 and vessel area percentage the prepared discs were slashed into blocks, and transverse sections of 14 μm in thickness were made by a sliding microtome (along the two cardinal directions). Transverse sections were stained with safranin, dehydrated through a series of ethanol, and then mounted on slides. Transverse images were obtained using a digital camera (Nikon DS-5M) connected to a light microscope (Axioscop; Carl Zeiss, Jena, Germany).

Two cross-sectional areas, 1.5 or 2.5 mm^2, in the centre of annual rings, excluding broad and narrow rays, were selected for the measurement of vessel diameter, vessel number per mm^2 and vessel area percentage. Since vessel elements were not exactly circular, the diameter was calculated as the mean of maximum and minimum diameters.

For measurements of vessel element length and percentages of the perforation plate types, vessel elements were macerated by the method described originally by Franklin (1945). Wood chips, which were prepared from each annual ring, were soaked in a mixture of equal volumes of glacial acetic acid and hydrogen peroxide and heated at 60°C for 72 hours. The whole lengths of one hundred vessel elements were measured, including the tails (Kitin et al. 1999). To measure the percentages of perforation plate types, the frequency of each type (simple, scaliform and simple/scaliform) was determined among the one hundred vessel elements in each annual ring. Preliminary studies of the vessel elements anatomy showed that vessel number per mm^2, vessel area percentage, average vessel diameter and vessel element length in all annual rings from the pith side to the bark side were considerably different among the studied provenances (Bayramzadeh et al. 2008). By contrast, the percentages of perforation types did not differ noticeably. Therefore, relationships between the percentages of perforation plate types and climate factors were not discussed in this research.

Foliar analysis

Measurements of stomatal conductance and transpiration rate were carried out on six fully expanded leaves (sunned leaves from the middle part of the crown) in the early August, 2005. Stomatal conductance and transpiration rate were measured using LI-1600 Steady State Porometer (LI-COR, Inc., Lincoln, USA). Measurements were made on cloud-free days between 11:30 a.m. and 13:30 p.m. and repeated on five sunny days (Nardini, Salleo 2000; Uemura et al. 2000).

The leaves used for the measurement of stomatal conductance and transpiration rate were collected for morphological studies. Leaf areas (LA, cm^2) were determined on fresh ones by the image analysis software, ImageJ (National Institutes of Health, Maryland, USA). Leaves were dried at 80°C for 72 h and weighed for the calculation of dry mass per unit leaf area (LMA, mg·cm^{-2}). Small parts of leaves, which were fixed in FAA solution (50% ethanol:acetic acid:formaldehyde, 18:1:1, v/v), were hand-cut for measuring leaf thickness. Leaf thickness was measured by the image analysis software ImageJ.

For measurements of stomatal density (SD, stomatal number mm^{-2}) and stomatal pore length (SPL, mm), small squares (~5mm^2) of the leaves which were used for physiological studies were cut and placed in 5 ml of 30% H_2O_2 solution with 0.1 g of tetrasodium pyrophosphate and then were warmed at 35°C about one week (until all mesophyll tissue had disintegrated). Cuticles were removed from the solution, washed, stained with 1% safranin and examined under a light microscope (Hovenden, Brodribb 2000).

Climate data

Monthly means of precipitation and temperature (1971–2000) were extracted from the climate database generated by Japan Meteorological Agency, JMA (http://www.data.kishou.go.jp). Monthly means of precipitation and temperature from 1971 to 2000 were chosen, since this study was designed to find out the relations between vessel element anatomy, foliar traits and the climate conditions of the original seed sources in the past.

Our interest in this study was to clarify the relationships between anatomical characteristics of vessel elements, different foliar traits and simple climate factors for which figures are readily obtainable.

Statistical analysis

Statistical analyses were carried out with StatGraphics Plus 5.1 (Stat Point, Inc., Northern Virginia, USA). Correlation analysis was used to analyse the relationship between the climate factors and anatomical characteristics of vessel elements as well as different foliar traits.

RESULTS AND DISCUSSION

Table 2 shows the relationships between climatic factors and vessel number per mm^2, vessel area percentage, average vessel diameter plus vessel element length of annual ring number one (pith side) to annual ring number six (bark side). According to Table 2, vessel number per mm^2 showed a significant negative correlation ($n = 7$, $P < 0.05$) with yearly, winter, spring and autumn precipitations. The negative correlation between vessel number per mm^2 and precipitation was also reported for *Fagus lucida,* another diffuse porous hardwood from Fagaceae, by Fei et al. (2000) and for *Quercus* species including *Q. coccifera, Q. ilex* and *Q. faginea* by Salvador et al. (1997), which were very similar to our findings for *Fagus crenata* in this regard.

The vessel area percentage also showed a significant downward trend ($n = 7$, $P < 0.05$) against yearly, winter, spring and autumn precipitations. However, vessel number per mm^2 and vessel area percentage did not show any noticeable relationships with the summer precipitation. Detailed studies on the seasonal precipitation of the studied provenances revealed that the amount of winter precipitation was considerably different among the provenances (Table 1). The range of winter precipitation was between 89 mm (Chichibu) and 835 mm (Nishikawa). This difference in the amount of winter precipitation resulted from the amount of snowfall. The Sea of Japan side of Honshu receives the heaviest snowfalls in the world for a region close to 40°N latitude (Matsui et al. 2004). Mean snow depth in this region generally exceeds 1 m and frequently can be up to 3 m in the mountains (Peter 1997). Furthermore, snow often remains until June (Tanaka 1987). Therefore, it seems that the amount of snowfall is likely to induce the amount of wet soil in the spring, when the cambial activity is started, and consequently the amount of transportable water. In addition, this difference in the amount of transportable water might influence the vessel number per mm^2 and vessel area percentage in *Fagus crenata.*

The studied anatomical characteristics of vessel elements did not show a significant relationship with summer precipitation (Table 2). This finding for *Fagus crenata* was not in agreement with the findings of Sass and Eckstein (1995) for *Fagus sylvatica,* which revealed the importance of summer precipitation for the vessel formation in *Fagus sylvatica*. These varied results are likely to be associated with the fact that in contrast to the *Fagus* occurrences on the other continents where summer can be dry, rainfall during the summer season is generally sufficient for *Fagus crenata* throughout the Japanese islands (Tanaka, Taoda 1996).

As mentioned earlier, vessel number per mm^2 and vessel area percentage in examined annual rings within the sapwood area of the samples which were prepared from different provenances and grown under uniform environmental conditions showed a significant correlation with the yearly, winter, spring and autumn precipitations of the original provenances (Table 2). Therefore, it can be suggested that vessel number per mm^2 and vessel area percentage in *Fagus crenata* are genetically variable against precipitation of the origins, however vessel diameter and vessel element length are not

Table 2. The correlation coefficient (r) of vessel number per mm^2, vessel area percentage, average vessel diameter and vessel element length with yearly precipitation (YP), spring precipitation (SP), summer precipitation (SUP), autumn precipitation (AUP), winter precipitation (WP), mean annual temperature (MAT), mean spring temperature (ST), mean summer temperature (SUT), mean autumn temperature (AUT) and mean winter temperature (WT) in annual ring number one (pith side) – annual ring number six (bark side) in studied provenances of *Fagus crenata*

		YP	SP	SUP	AUP	WP	MAT	ST	SUT	AUT	WT
				(mm)					(°C)		
Vessel number (mm^{-2})											
Annual ring number	one	−0.90**	−0.70*	−0.52	−0.91**	−0.84*	0.17	0.55	0.37	0.47	0.42
	two	−0.80*	−0.75*	−0.43	−0.88**	−0.75*	0.44	0.61	0.44	0.54	0.49
	three	−0.85**	−0.78*	−0.55	−0.86**	−0.80*	0.43	0.51	0.37	0.42	0.36
	four	−0.75*	−0.79*	−0.18	−0.78*	−0.75*	0.27	0.52	0.40	0.42	0.37
	five	−0.80*	−0.81*	−0.20	−0.75*	−0.76*	0.50	0.56	0.42	0.45	0.40
	six	−0.76*	−0.79*	−0.28	−0.77*	−0.76*	0.51	0.65	0.47	0.55	0.51
Vessel area percentage											
Annual ring number	one	−0.96**	−0.84*	−0.59	−0.82*	−0.96**	0.16	0.60	0.35	0.53	0.54
	two	−0.80*	−0.75*	−0.31	−0.88**	−0.75*	0.02	0.55	0.37	0.53	0.51
	three	−0.84*	−0.76*	−0.38	−0.85**	−0.92**	0.22	0.44	0.31	0.42	0.39
	four	−0.76*	−0.77*	−0.16	−0.75*	−0.83*	0.15	0.60	0.45	0.50	0.47
	five	−0.84*	−0.75*	−0.20	−0.77*	−0.92**	0.17	0.70	0.61	0.63	0.55
	six	−0.75*	−0.76*	−0.37	−0.75*	−0.75*	0.51	0.48	0.27	0.37	0.33
Average vessel diameter											
Annual ring number	one	0.29	0.29	0.24	0.40	0.36	−0.03	−0.25	−0.11	−0.33	−0.37
	two	0.13	0.03	0.10	0.35	0.27	−0.67	−0.65	−0.69	−0.59	−0.56
	three	0.10	0.01	0.23	0.21	0.36	−0.67	−0.25	−0.06	−0.21	−0.29
	four	0.02	0.16	0.02	0.39	0.49	−0.24	−0.04	−0.03	−0.15	−0.19
	five	0.18	0.22	0.07	0.28	0.50	−0.32	−0.02	−0.05	−0.13	−0.14
	six	0.37	0.07	0.18	0.26	0.01	−0.37	−0.27	−0.16	−0.18	−0.21
Vessel element length											
Annual ring number	one	−0.27	−0.31	−0.59	−0.32	−0.20	0.34	0.53	0.51	0.49	0.42
	two	−0.19	−0.06	−0.23	−0.09	−0.56	0.10	0.10	0.15	0.03	0.01
	three	−0.21	−0.32	−0.10	−0.26	−0.42	0.16	0.34	0.32	0.22	0.15
	four	−0.02	−0.27	−0.15	−0.21	−0.40	0.05	0.30	0.25	0.18	0.12
	five	−0.25	−0.45	−0.32	−0.29	−0.44	0.02	0.46	0.45	0.33	0.26
	six	−0.20	−0.44	−0.18	−0.32	−0.42	0.06	0.43	0.42	0.32	0.24

Data are means from 1971–2000; $^{**}P < 0.01$; $^{*}P < 0.05$

variable. A way of interpreting different trends by the vessel element anatomical features against the past precipitation data of the origins is to consider that some anatomical features like vessel number per mm^2 were influenced by precipitation and these specific characteristics persisted, as they could be genetically fixed, but some of them were not.

In response to the temperature, the anatomical characteristics of vessel elements show a significant relationship neither with mean annual temperature of the original provenances nor with mean seasonal temperatures in all annual rings (Table 2). Thus, it can be noted that the anatomical characteristics of vessel elements in *Fagus crenata* are not genetically variable against the temperature of the seed sources.

As mentioned earlier, previous research showed that the variations of the anatomical characteristics of vessel elements within the sapwood area were in correspondence with the variation of the different foliar traits in *Fagus crenata* (Bayramzadeh

Table 3. The correlation coefficient (*r*) of the foliar traits with yearly precipitation (YP), spring precipitation (SP), summer precipitation (SUP), autumn precipitation (AUP) and winter precipitation (WP) mean annual temperature (MAT), mean spring temperature (ST), mean summer temperature (SUT), mean autumn temperature (AUT) and mean winter temperature (WT) in studied provenances of *Fagus crenata*

	YP[1]	SP	SUP	AUP	WP	MAT	ST	SUT	AUT	WT
			(mm)					(°C)		
E ($\mu g\ cm^{-2}\cdot s^{-1}$)	–0.85**	–0.76*	–0.41	–0.80*	–0.85**	0.67	0.73	0.62	0.65	0.59
g_s ($cm\cdot s^{-1}$)	–0.81*	–0.78*	–0.21	–0.80*	–0.87**	0.65	0.74	0.65	0.65	0.59
LA (cm^2)	0.32	0.52	0.40	0.26	0.18	–0.88**	–0.87**	–0.93**	–0.85*	–0.83*
LT (mm)	–0.93**	–0.84*	–0.52	–0.86**	–0.90**	0.60	0.69	0.52	0.59	0.55
LMA ($mg\cdot cm^{-2}$)	–0.91**	–0.76*	–0.39	–0.88**	–0.94**	0.59	0.68	0.50	0.58	0.54
SD (NO mm^{-2})	–0.42	–0.54	–0.06	–0.42	–0.49	0.68	0.74	0.73	0.66	0.57
SPL (μm)	–0.63	–0.50	–0.34	–0.55	–0.66	–0.13	–0.06	–0.35	–0.10	–0.05

E – transpiration rate; g_s – stomatal conductance; LA – leaf area; LT – leaf thickness; LMA – leaf dry mass per area; SD– stomatal density; SPL – stomatal pore length

Data are means from 1971–2000; ***P* < 0.01; **P* < 0.05

et al. 2008). Therefore, in the present research exploring the ecological patterns on an almost whole tree level, the relationships between different foliar traits and climatic factors were also examined. Table 3 shows the relationships between the studied foliar traits with yearly and seasonal precipitations and temperatures. According to Table 3 transpiration rate, stomatal conductance, leaf thickness and leaf dry mass per unit leaf area showed a significant negative correlation with yearly, spring, autumn and winter precipitations ($n = 7$, $P < 0.05$). As mentioned before, the amount of snowfall differed considerably among the provenances. Therefore, it seems that the amount of snowfall is likely to induce the amount of transportable water which has to be transferred from stem to leaves by vessel elements and from leaves to atmosphere by stomatal functions. Therefore, it can be suggested that variations of yearly, spring, autumn and winter precipitations are mainly associated with variations of the transpiration rate and stomatal conductance in *Fagus crenata*.

Similar trends between precipitation and transpiration rate, stomatal conductance, leaf thickness as well as leaf dry mass per unit leaf area may be due to the fact that transpiration rate and stomatal conductance were highly correlated with leaf thickness ($r = 0.90$ and 0.92) and leaf dry mass per unit leaf area ($r = 0.95$ and 0.96).

According to Table 3 transpiration rate, stomatal conductance, leaf thickness and leaf dry mass per unit leaf area did not show a significant correlation with mean annual and seasonal temperatures ($n = 7$, $P < 0.05$). Therefore, it can be noted that the above-mentioned foliar characteristics in *Fagus crenata* are genetically variable against the precipitation of the seed sources; however they are not variable against the temperature.

Stomatal density and stomatal pore length showed negative trends against yearly and seasonal precipitations, however their relations were not significant not only with the yearly precipitation but also with the seasonal precipitation (Table 3). Stomatal density and stomatal pore length did not show a noticeable relation with the mean annual and seasonal temperatures of the origins, either. Therefore, it could be suggested that other factors or the combination of the several climatic factors are responsible for the variation of stomatal characteristics.

Leaf area showed significant relationships neither with the yearly precipitation nor with the seasonal precipitation (Table 3). By contrast, it showed a significant relationship with mean annual and seasonal temperatures (Table 3).

The highly correlated relationships between mean spring and summer temperature with leaf area revealed that leaf area was influenced by the temperatures of the growing season in *Fagus crenata.* As *Fagus crenata* is a deciduous broadleaved species, the correlation between mean autumn and winter temperature with leaf area may be due to the fact that mean summer and spring temperatures are positively correlated with mean autumn (r = 0.95, and 0.96; $P < 0.01$) and winter temperatures (r = 0.91, and 0.97; $P < 0.01$).

According to the above-mentioned results, it seems that anatomical characteristics of vessel elements and different foliar traits in *Fagus crenata* are influenced by climatic factors of the original provenances and the winter precipitation is the most important factor in this regard. However, multisite common garden experiments with the large number of samples would be needed in order to generalize the findings for *Fagus crenata* in Japan.

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